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THE GENETIC EVALUATION OF A TAXONOMIC CHARACTER IN DITHYREA (CRUCIFERAE)

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Developing accuracy in the evaluation of plant characters and characteristics for taxonomic purposes is a long-standing problem. When differences are found between groups of plants which otherwise appear to be related, the immediate question arises as to what these differences mean. Specifically, what do the differences mean in terms of the genetic make-up of the natural group to which such plants belong and how valuable are they as taxonomic criteria? In our efforts to interpret speciation in relation to a given species or a group of species, we wish to rely upon those characters as indicators of relationship (or lack of it) that are so deeply seated in the genetic constitution of the species that they cannot be easily obliterated or greatly modified by the direct effects of any given simply segregating factor or combination of segregating factors. In general, the kinds of characteristics that offer the greatest possibilities for taxonomic reliability are those that are dependent upon a multiplicity of genes and gene combinations for their ultimate expression—genes that are not in a single linear sequence of interdependency, but genes in many series whose interaction in a highly complex way results in the final structure or function. It may also be suggested that any given characteristic thus dependent upon a complex genetical system, which is deeply situated within the genotype, becomes protected from radical changes by the build-up of interdependencies between it and other characteristics, some of which may be vital to survival. Thus the species phenotype persists over many generations, little altered in basic pattern by the

numerous minor segregations that account for the usual variation present.

At the other end of the scale, characteristics under the control of the simplest gene systems are expected to be least reliable as the basis for classification. Such characteristics would be easily modified or suppressed by repetitious mutations, gene rearrangements or by ordinary segregation. In consequence, it is probably accurate to say that the more simply a character-difference is inherited, the less reliable it is as a criterion of speciation. The converse of this proposition, that the greater the complexity of inheritance of a character-difference the more reliable it is as a criterion of speciation, seems equally tenable. In trying to evaluate a given genetically controlled characteristic, an important attack on the problem is to determine the relative complexity of its inheritance.

One reason that taxonomic characters *per se* have not been frequently subjected to genetic analyses is that this is very time consuming and relatively unrewarding. The results of such experimental work, though answering the specific question regarding the nature of the taxonomic character, often do not have broader implications. Generalizations can only rarely be made because the applicability is or may be restricted to the immediate group under investigation. However, it is important for the long term to have many more cases worked out than are now known. Ultimately these will provide safe guides to proper character-evaluations, which is one of the current needs of taxonomy.

In working with the *Cruciferae* over a period of years, I have often encountered situations where "presence" or "absence" of trichomes appeared to be of trivial significance (1940, 1952). However, without actually testing a given case, it was not possible to know whether the absence of an indument in a given population, in an otherwise pubescent species, was environmentally induced or whether it was under genetic control. An opportunity to experiment with the presence and absence of a dense covering of trichomes on the fruits of *Dithyrea Wislizenii* Engelm. came when a population of this species was found having both glabrous- and pubescent-fruited types growing together near Sacaton, Arizona. The fruits of individual plants of both the glabrous type and the pubescent type were collected

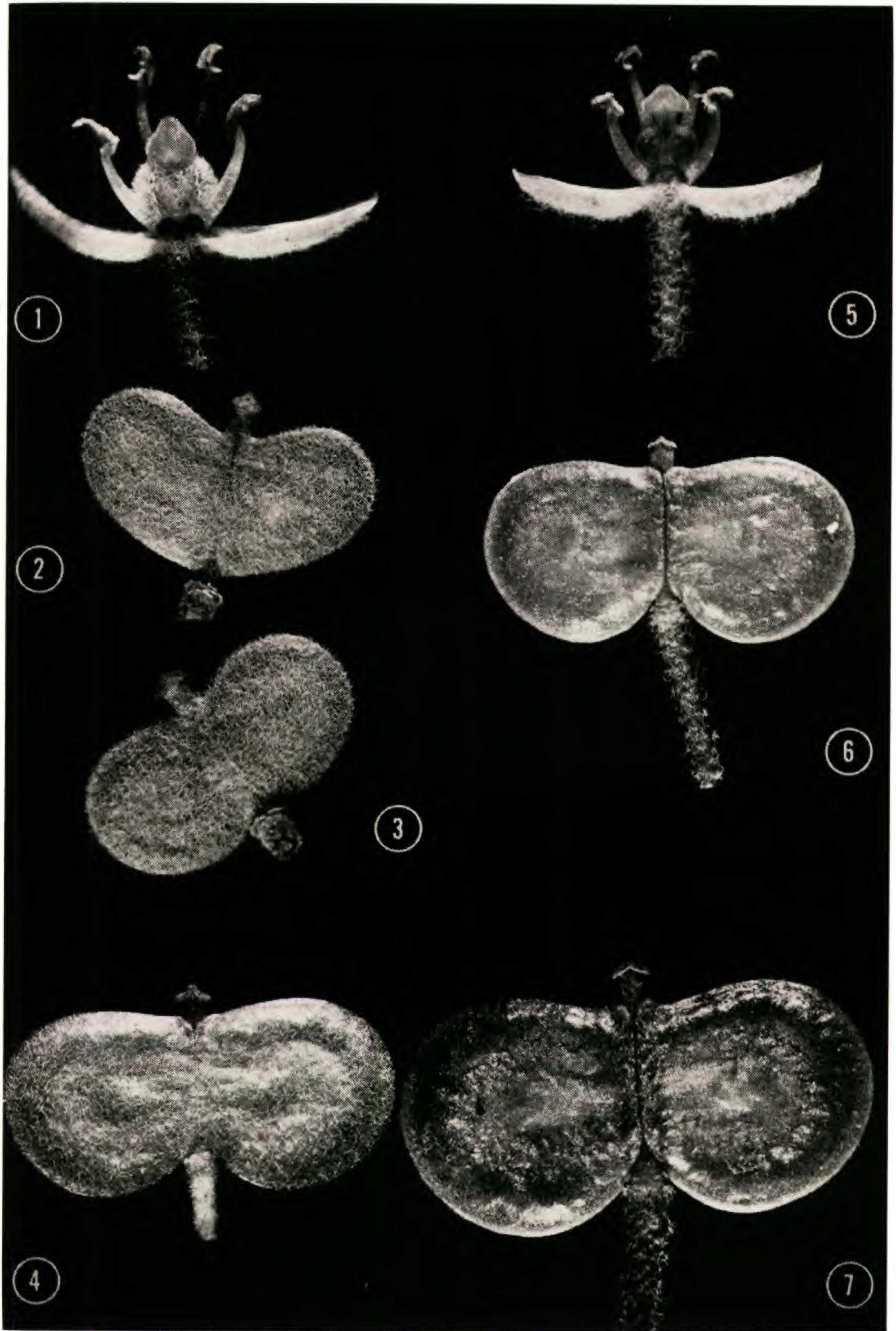


PLATE 1233. Flowers and fruits of *Dithyrea Wislizenii* Engelm. Fig. 1-4, a developmental series from flower to mature fruit of a pubescent-fruited type. In fig. 1, the petals, 2 sepals and the 2 near stamens have been removed to make the ovary visible. The same applies to fig. 5. Fig. 5-7, a developmental series from flower to mature fruit of a glabrous-fruited type.

and kept separate for testing purposes. The difference between the glabrous siliques and pubescent siliques is very striking, as may be seen in Plate 1233. The objective of the following experiments was to determine the genetic nature of glabrous vs. pubescent siliques in this species.

THE WILD POPULATION

The species, *Dithyrea Wislizenii*, extends from western Oklahoma and Texas to southern Utah and Nevada, and to Arizona and northeastern Mexico. It is common in sandy and loose granitic soils and often forms large stands composed of several thousands of individuals. Up to the present, a single glabrous-fruited *Dithyrea*, presumably closely related to *D. Wislizenii*, has been recognized as being of some taxonomic worth. Wooton and Standley (1913) originally described it at the species level as *D. Griffithsii* and it was later reduced to varietal rank by Payson (1918) under *D. Wislizenii*. In the Sacaton population, which provided the material for the following experiments, most of the plants possessed pubescent fruits, but there was a goodly number of glabrous-fruited individuals. Circumstances did not permit a definite count of pubescent vs. glabrous plants in the wild population. However, a rough estimate was recorded suggesting that the pubescent type predominated at least three to one. There were no intergrades. The wild plants possessed either glabrous fruits or pubescent fruits and none showed a gradation from one condition to the other.

PROGENY TEST OF SEED PARENTS

Four lots of seeds from the wild population were grown to provide plants for crossing purposes. Each seed lot came from a single wild plant, which had been open pollinated under natural conditions. The plants of culture numbers C-1 and C-4 were produced from glabrous-fruited parents, C-2 and C-3 were from

TABLE I

WILD PLANTS		PROGENIES	
<i>Plant No.</i>	<i>Siliques</i>	<i>No. Glabrous</i>	<i>No. Pubescent</i>
C-1	glabrous	9	3
C-2	pubescent	0	15
C-3	pubescent	0	10
C-4	glabrous	5	9

pubescent-fruited parents. Table I gives the classification of the plants of each culture.

It is of some interest that the progenies of both pubescent plants turned out to be uniformly pubescent even though there had been no pollen control on the parent plants.

Pollen mother-cell smears were made to reveal the chromosome number of both glabrous and pubescent plants. In each case the number $n = 5$ was found.

CROSSES AND RESULTS

Three types of crosses were made using various combinations from the four cultures originally grown from the wild plants listed in Table 1. These were glabrous \times glabrous, glabrous \times pubescent, and pubescent \times pubescent. In addition, 14 pubescent plants were placed together in an isolated greenhouse where interpollination was permitted to be effected by the insects normally present. In each of the three types of controlled crosses, bagging with muslin, emasculation and hand pollination were practiced. Controls to check the procedures were carried along with the experiments. These showed that pollen control was effective. All crosses were carried out reciprocally. Essentially the same results were achieved regardless of the direction in which the pollen was carried except for the reciprocal of

TABLE 2. GLABROUS \times GLABROUS

CROSS	PROGENY			3:1 RATIO	CHI-SQUARE
	No. <i>plants</i>	No. <i>glabrous</i>	No. <i>pubescent</i>		
C1-1 \times C1-3	17	12	5		
reciprocal	7	5	2		
	—	—	—		
	24	17	7	18:6	.16
C1-4 \times C4-9	20	15	5		
reciprocal	6	4	2		
	—	—	—		
	26	19	7	19.5:6.5	.05
C1-7 \times C4-7	12	9	3		
reciprocal	8	7	1		
	—	—	—		
	20	16	4	15:5	.266
	—	—	—		—
Total	70	52	18		.287
					P = .98-.95

pubescent C1-5 ♀ × glabrous C1-7 ♂. In this case, the reciprocal did not produce any filled seeds. The significance of this failure was not determined.

In addition to the results shown in Tables 2, 3 and 4, fourteen progenies of pubescent plants open pollinated from pubescent plants were grown. These amounted to 159 plants, all of which possessed pubescent siliques.

TABLE 3. GLABROUS × PUBESCENT

CROSS	PROGENY			1:1 RATIO	CHI-SQUARE
	No. <i>plants</i>	No. <i>glabrous</i>	No. <i>pubescent</i>		
C1-7 × C1-5	0	0	0		
reciprocal	10	3	7		
	—	—	—		
	10	3	7	5:5	1.60
C1-6 × C4-8	12	3	9		
reciprocal	11	4	7		
	—	—	—		
	23	7	16	11.5:11.5	3.52
C4-13 × C4-6	6	4	2		
reciprocal	14	5	9		
	—	—	—		
	20	9	11	10:10	.20
C4-10 × C4-14	17	6	11		
reciprocal	6	3	3		
	—	—	—		
	23	9	14	11.5:11.5	1.08
Total	76	28	48		6.40
					P = .2-.1
Pooled Chi-square (1 df)					5.26
					P = .05-.02
Heterogeneity Chi-square (3 df)					1.14
					P = .3-.7

The results are easily explainable if it is assumed that a single gene pair is operative in producing the glabrous or pubescent condition of the siliques. From the data, it is obvious that the pubescent plants are homozygous and recessive. Thus the genotype of the pubescent plants may be designated *gg*. When such a plant is crossed with a glabrous heterozygous individual (*Gg*), the resulting progeny should show a 1:1 ratio of glabrous to pubescent plants. In table 3, results from four different crosses between glabrous and pubescent plants are given and the Chi-square test for goodness of fit to a 1:1 ratio is provided. The

TABLE 4. PUBESCENT \times PUBESCENT

CROSS	PROGENY	
	<i>No. glabrous</i>	<i>No. pubescent</i>
C2-7 \times C2-8	0	11
reciprocal	0	1
	—	—
	0	12
C3-2 \times C3-9	0	10
reciprocal	0	8
	—	—
	0	18
C3-6 \times C3-7	0	13
reciprocal	0	28
	—	—
	0	41
C4-11 \times C4-12	0	17
reciprocal	0	30
	—	—
	0	47
Total	0	118

numbers of plants in the various progenies are small and the possibility of results different from those shown should perhaps not be ruled out completely. However, the evidence strongly favors a 1:1 ratio and the assumption of a heterozygous (*Gg*) plant as the glabrous parent in each cross seems justified.

If heterozygotes are crossed, a 3:1 ratio of glabrous to pubescent is to be expected. Table 2 gives the data on three glabrous \times glabrous crosses and the results show convincingly that a 3:1 ratio of glabrous to pubescent was obtained. It seems perfectly safe to assume that each of the six parents was of the constitution *Gg* with respect to the genes in control of the glabrous vs. pubescent condition. Evidently no homozygous dominant plants were used in the experiments. Such plants could not be distinguished from the heterozygotes phenotypically.

DISCUSSION

The mechanism of genetic control of glabrous vs. pubescent siliques in *Dithyrea Wislizenii* is obviously a relatively simple one. For this reason, it is safe to reject the phenotypic characteristic of glabrous siliques as having no significance for taxonomic purposes. Plants with this characteristic are expected to occur without respect to phylogenetic relationship in the populations of the species. In fact, this is exactly what one finds.

Glabrous-fruited plants are found in *D. Wislizenii* proper and in *D. Wislizenii* var. *Palmeri*. Furthermore, glabrous-fruited plants are found more or less throughout the geographical range of the species. On the basis of collections in the Gray Herbarium, the pubescent type appears to be more common than the glabrous. Collectors evidently distinguish between the glabrous and pubescent plants in the field because there are but three mixed collections among 84 different ones available in the herbarium. Six of the collections have glabrous fruits and 75 have pubescent fruits.

In my own field experience, I have examined four different populations of *D. Wislizenii*, one in Texas, two in Arizona and one in New Mexico. In three of these populations, I was unable to locate any glabrous-fruited plants. The fourth population yielded the material reported on above. This evidence added to that from herbarium material makes it quite clear that pubescent-fruited plants predominate in the species. If pubescent siliques represent the homozygous recessive condition, as indicated by the analysis of the one population, a more prevalent occurrence of the glabrous type would be expected throughout the species as a whole unless there are positive factors operating to select against it. However, we have no way of knowing about this at the present time. One observation may be pertinent to any ultimate explanation for the prevalence of the pubescent-fruited type. It is that the plants of *D. Wislizenii* are self incompatible. The chances of the accidental establishment of predominantly glabrous-fruited populations through isolation are considerably reduced as compared with a self compatible species.

CONCLUSIONS

The glabrous-fruited condition in *Dithyrea Wislizenii*, which provided the chief basis for describing *D. Griffithsii* Wooton and Standley as a separate species, is a simply inherited characteristic under single gene control. Glabrous-fruited heterozygotes when crossed produce a simple mendelian 3:1 ratio of glabrous- to pubescent-fruited plants. Glabrous-fruited heterozygotes crossed with pubescent-fruited plants produce approximately a 1:1 ratio of glabrous to pubescent plants. Pubescent-fruited plants crossed with each other produce only pubescent-fruited offspring. The pubescent plants studied all proved to be